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# Comparative Anatomy of the Nectaries of *Aglaomorpha* and *Drynaria* (Polypodiaceae)

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ABSTRACT.—The anatomy of the foliar nectaries of four drynarioid species (*Drynaria quercifolia*, *D. rigidula*, *Aglaomorpha coronans* and *A. acuminata*) is described. The nectaries of all four species are vascularized modifications of the leaf blade and are distinct from surrounding tissue. They are composed of densely staining tissue with small isodiametric cells and reduced intercellular spaces. The nectaries of *D. quercifolia* and *A. coronans* occur as patches of tissue on the leaf blade. In contrast, the nectaries of *D. rigidula* and *A. acuminata* are stand-alone structures. The nectaries of *A. acuminata* represent the most specialized nectaries yet described among the ferns. The contribution of these data to cladistic analyses of *Drynaria* and *Aglaomorpha* is discussed.

KEY WORDS.—Nectary anatomy, *Aglaomorpha*, *Drynaria*

Drynarioid ferns are a monophyletic grouping of 30 species now classified in two genera, *Aglaomorpha* and *Drynaria* (Roos, 1985; Janssen and Schneider, 2005) in the Polypodiaceae. The ferns are epiphytic, they occur in the paleotropics (Copeland, 1947; Holttum, 1968) and many species have humus-collecting nest leaves in addition to photosynthetic foliage leaves (Holttum, 1968; Janssen and Schneider, 2005). A distinctive characteristic of drynarioid ferns is the presence of specialized nectar-secreting glands on the leaves (Copeland, 1947; Holttum, 1968; Koptur *et al.*, 1982; Elias, 1983; Roos, 1985; Janssen and Schneider, 2005).

Drynarioid nectaries are described as translucent spots located close to the junction of the costa/rachis and occurring in the lobes of petiolar wings. The *Aglaomorpha acuminata* (Willd.) Hovenkamp nectary is situated on a "specialized quadrangular extension" (Roos, 1985). Drynarioid nectary anatomy and morphology is rarely noted in detail. It has been described only briefly as a grouping of columnar cells with an associated plexus of vascular tissue (Nayar, 1961).

> "Nectaries occur irregularly distributed close to the midrib and some of the main lateral veins of the lamina. The nectaries are irregularly oval or circular, pellucid to yellowish areas in the lamina, and in very young leaves secrete a viscous, sweet, sometimes bad smelling liquid. They are composed of compactly placed glandular cells which are columnar and noncholorophylous. A vascular plexus formed by intersecting veinlets and composed of diffused vascular tissue occurs towards the center of each nectary."

Additionally, the distribution of nectaries on leaves of ten drynarioid species has been described and three distribution patterns were identified (Zamora and Vargas, 1974). The secretion of liquid from various drynarioid

species, including *Drynaria rigidula* (Sw.) Bedd. has been confirmed to be nectar (Koptur *et al.*, 1982).

In this study, the anatomy of the foliar nectaries of four species of drynarioid ferns (*A. acuminata*, *A. coronans* (Wall. ex Mett) Copel., *Drynaria quercifolia* (L.) J. Sm. and *D. rigidula*) is described. These data are compared within the group and to nectaries of *Pteridium*, another fern species with nectaries. The data are then discussed in the context of the most recent cladistic analysis (Janssen and Schneider, 2005).

Nectaries vary widely in anatomy, secretion method and location on the plant (Fahn, 1979; Elias, 1983). Various types of extrafloral nectaries have been described based on anatomical structure, including a number of which occur on foliage leaves, like those of drynarioid ferns (Zimmerman, 1932). This diversity of nectaries is strong evidence that they have evolved many times throughout the history of flowering plants and ferns (Elias, 1983).

Other ferns that bear nectaries include the common bracken fern (*Pteridium*) (Darwin, 1877; Page, 1982; Power and Skog, 1987; Rumpf *et al.*, 1994) and *Cyathea* (pers. comm. White, 2007). In *Polypodium*, *P. myriolepis* Christ, *P. pyrrholepis* (Fée) Maxon, *P. rosei* Maxon, *P. sanctae-rosae* (Maxon) C.Chr. and *P. thyssanolepis* A.Br. ex Klotzsch were also observed to secrete nectar (Koptur *et al.*, 1982). Among the ferns, the anatomy of nectaries of *Pteridium* has been studied in the most detail.

Based on combined molecular and morphological evidence, a recent study concludes that the genus *Drynaria* is paraphyletic and that *Aglaomorpha* is a monophyletic group derived from within it (Fig. 1) (Janssen and Schneider, 2005). Despite these findings, the morphological data, alone, do not support a paraphyletic *Drynaria*. Although the presence and position of drynarioid fern nectaries are used as character states in the analysis (Janssen and Schneider, 2005), it does not take into account possible differences in nectary anatomy. As anatomical data are important for phylogenetic reconstruction (Kaplan, 1984), using nectary anatomy as a character state may help to clarify the morphological data set.

## Materials and Methods

Young nectary-bearing leaves of each of three species (*Drynaria quercifolia*, *Drynaria rigidula*, *Aglaomorpha acuminata*) were collected from the Duke University greenhouse. Due to the absence of young material, mature leaves were used for the fourth species, *Aglaomorpha coronans*. The nectaries were cut from the leaves of each species and then preserved in formalin-acetic acid alcohol (FAA) and dehydrated in a tertiary butyl alcohol series (Johansen, 1940). Voucher specimens for the species are deposited in the Duke Herbarium (DUKE).

The leaf material of *D. quercifolia*, *D. rigidula*, and *A. speciosa* was imbedded in paraffin using standard techniques (Johansen, 1940). Paradermal and cross sections of 10 μm were made of the entire gland of each species. Sections were then mounted onto slides and stained with safranin and fast

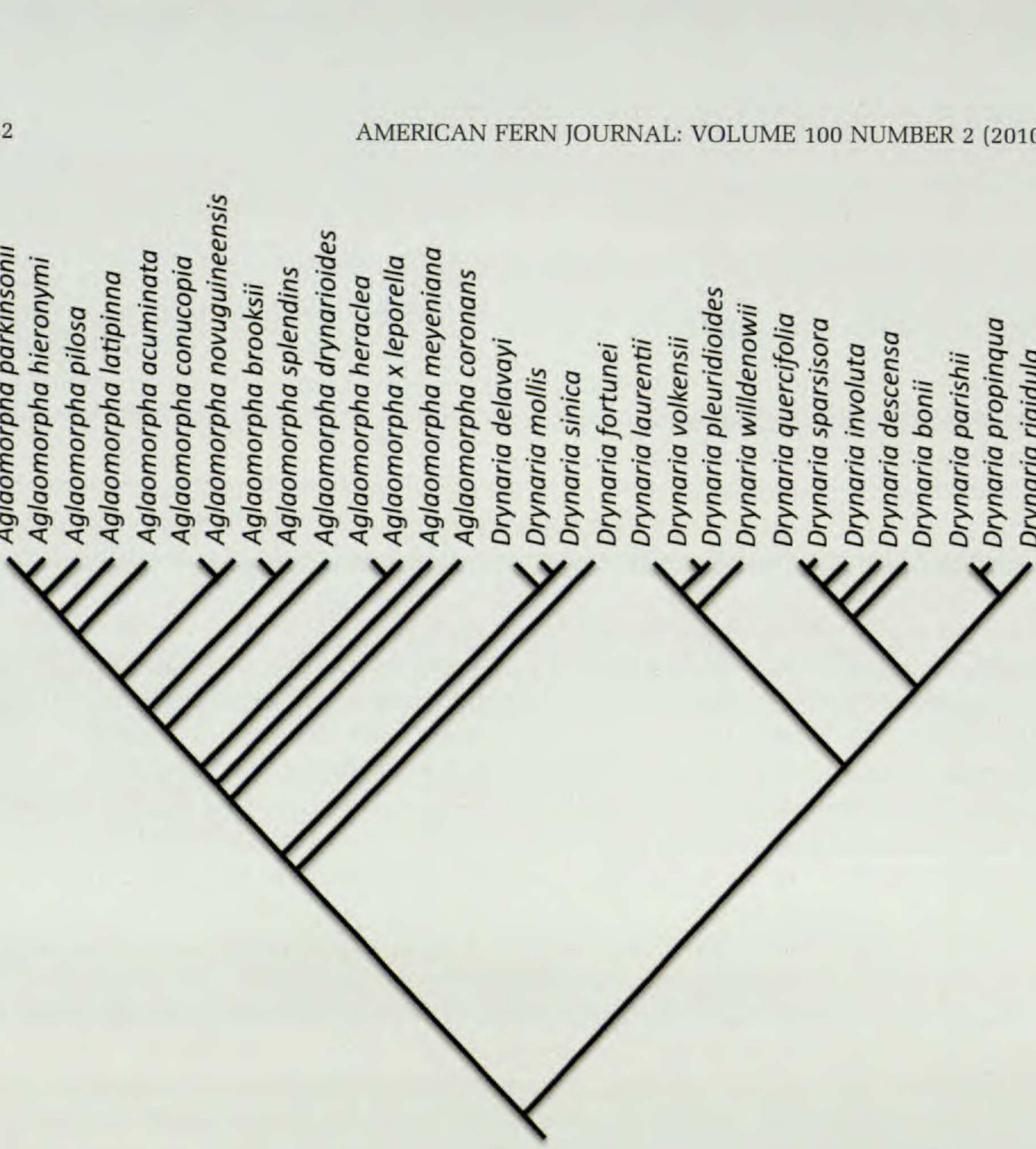
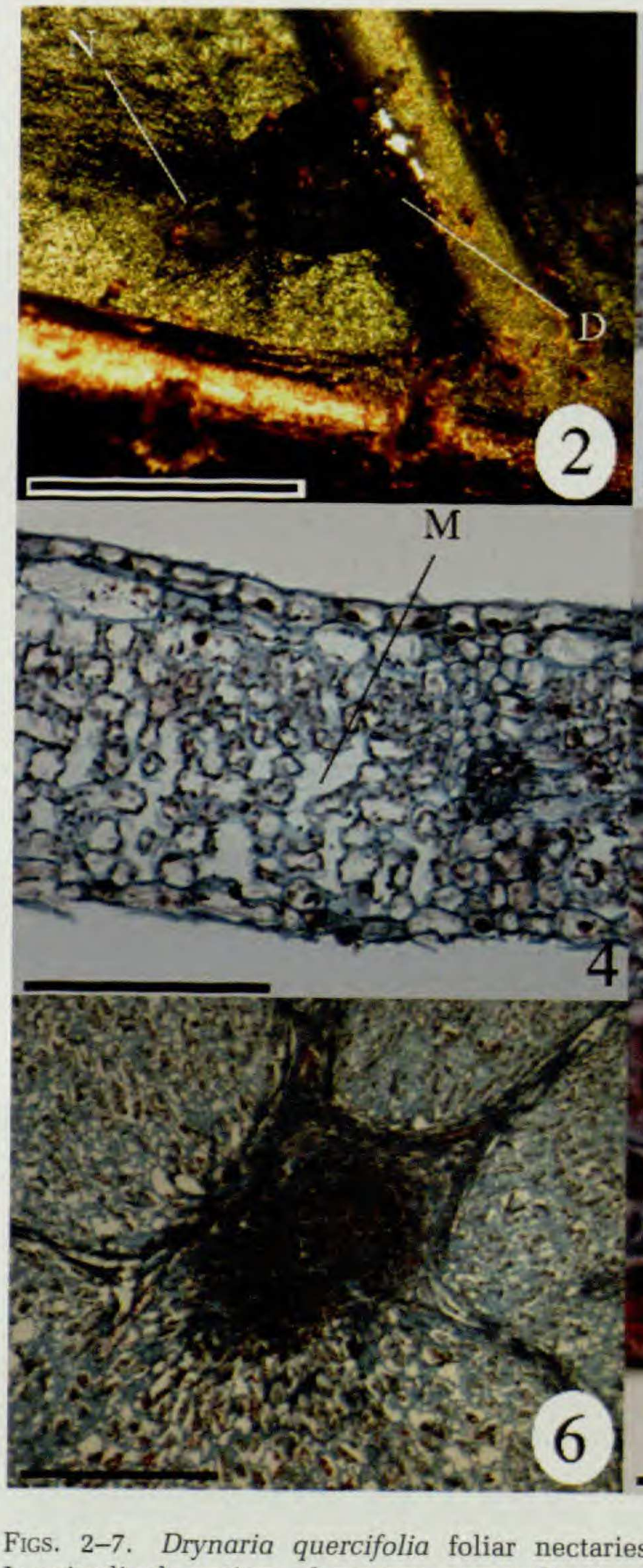



FIG. 1. Phylogenetic tree from (with permission) Janssen and Schneider (2005). Based on the strict consensus tree of the two most parsimonious trees with the combined data set (morphological and genetic).

green. Samples of *A. coronans* were mature leaves and using the standard technique did not produce quality sections. Longitudinal hand-sections were made of these glands. All of the slides were examined using a standard light microscope and digital images were prepared and labeled using Adobe Photoshop. Measurements were made using a stage micrometer.

## RESULTS

*Drynaria quercifolia.*—Nectaries are present on both foliage leaves and nest leaves. The glands are translucent patches approximately 1–2 mm in diameter. Clear liquid was observed on the abaxial surface of the glands (Fig. 2). On the foliage leaf they occur at the junction of lateral veins with the main vein, although a nectary does not occur at every junction. When they do occur, glands are present distal to the junction. The nectaries continue down the




FIGS. 2–7. *Drynaria quercifolia* foliar nectaries. 2. Nectary on abaxial surface of leaf. 3. Longitudinal section of nectary perpendicular to rachis. 4. Longitudinal section of leaf. 5. Longitudinal section of the nectary perpendicular to the rachis. 6. Paradermal section of gland. 7. Longitudinal section of stomata on abaxial surface of the nectary. Bar in 2 = 2 mm; bars in 3, 4, 6 = 5 μm; bar in 5 = 2 μm; bar in 7 = 0.5 μm; N = nectary; D = droplet; M = spongy mesophyll; S = stomata; V = vascular bundle.

petiole at regular intervals in the absence of an associated leaf lobe. In addition, smaller nectaries, less than 1 mm in diameter, occur on the leaf lamina with no regular pattern although they occasionally occur in clusters. The nest leaves also bear nectaries.

In cross-section, the nectary extends from the adaxial surface of the leaf to the abaxial surface. There is no variation in the thickness of the leaf although there are more layers of cells in the nectary than in the surrounding leaf blade (Fig. 3). The nectariferous tissue of *D. quercifolia* is distinct from surrounding leaf tissue (Fig. 4). The cells in the glandular region are darkly staining and approximately 0.4 μm smaller in diameter than the leaf lamina cells. Plastids in the glandular cells are non-green and the glandular region lacks prominent intercellular spaces (Figs. 5 and 6) whereas intercellular spaces are prominent in the leaf mesophyll (Fig. 4). Nectaries are bordered by specialized branches of vascular tissue (Figs. 5 and 6). These veins come into direct contact with the glandular region and contain both xylem and phloem. Stomates are present on the abaxial surface of the nectary (Fig. 7).

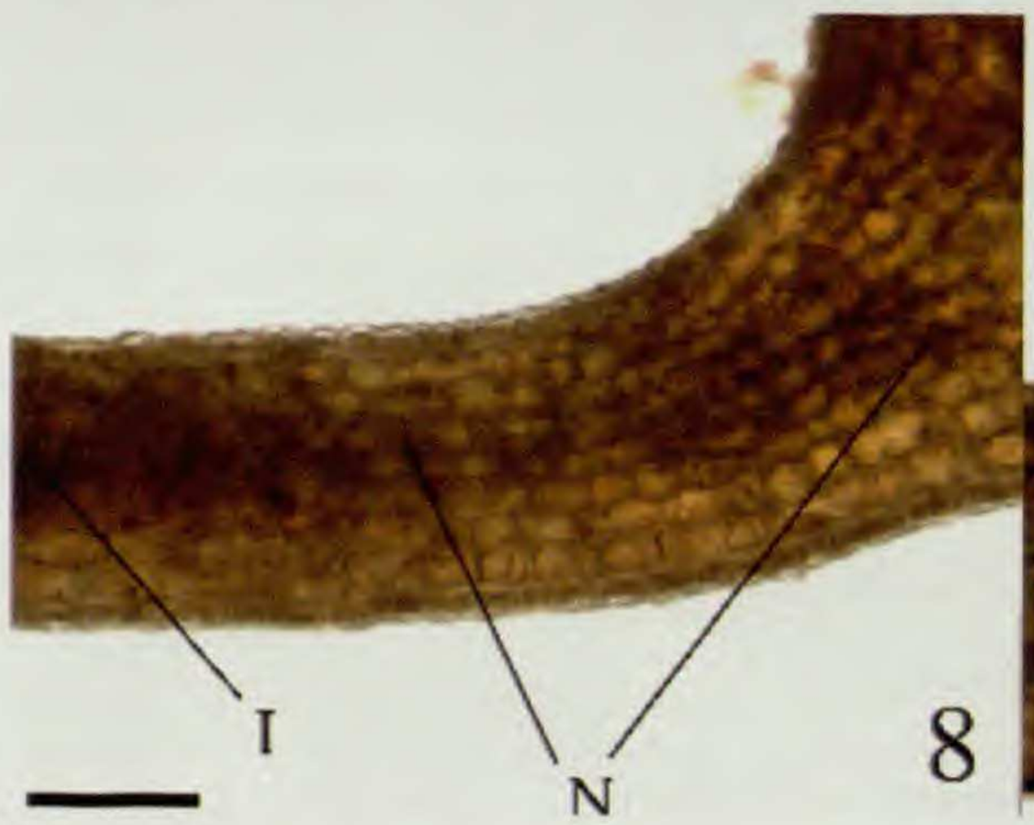
*Aglaomorpha coronans*.—Nectaries are approximately 2 mm in diameter, occur distal to the junction of the main vein with a lateral vein and are visible as translucent spots or patches in the abaxial surface of the leaf tissue. They are not present at every junction. Smaller nectaries, less than 1 mm in diameter, that are not associated with the main vein were observed on the leaf lamina. They occur individually and in groups, and are scattered throughout the leaf blade.

Hand sections of the larger nectaries (Fig. 8) reveal a glandular region of clear cells distinct from the surrounding leaf blade (Fig. 9). The glandular tissue lacks prominent intercellular spaces and its cells are approximately 0.1 μm smaller in diameter than those of the leaf blade.

The nectaries not associated with the main (Fig. 10) vein lack chlorophyll and prominent intercellular spaces. They are composed of cells approximately 0.1 μm smaller in diameter than cells of the leaf blade tissue (Fig. 11). They are also different from the larger glands because they are composed of the same number of cell layers as the surrounding unmodified leaf tissue. As a result, the thickness of the leaf at the gland is less than that of the surrounding non-glandular region.

*Drynaria rigidula*.—Nectaries of this species occur on the basiscopic side of leaflets. They are concavities on the abaxial surface of the leaflet base with an approximate diameter of 0.5–1 mm. The depression is formed by the midvein on one side of the nectary and a secondary vein on the opposite side. Clear liquid was observed on the abaxial surface of most nectaries and glands appeared to be more active on the basal half of fronds. Dark-colored mold was often observed on the nectaries (Fig. 12). Similar nectaries occur on the petiole of the frond in the absence of leaflets.

The nectariferous cells (Figs. 13 and 14) are approximately 0.03 μm smaller in diameter than those of the leaf (Fig. 15). Unlike this surrounding leaf blade tissue, the glandular cells lack prominent intercellular spaces and plastids in the nectary are non-green (Fig. 14). Vascular tissue does not branch into the

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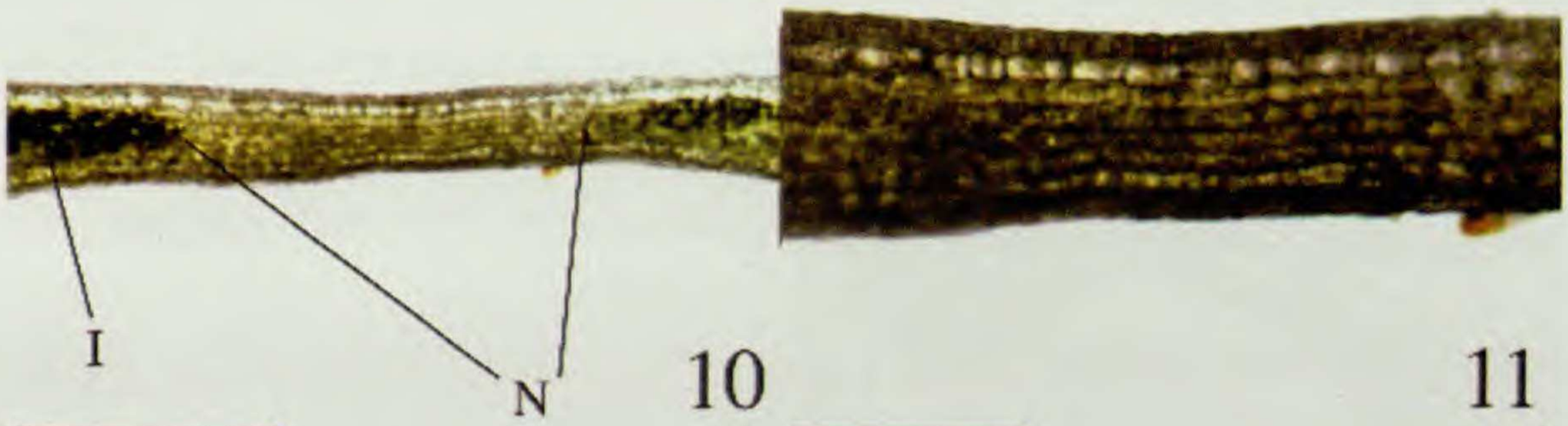


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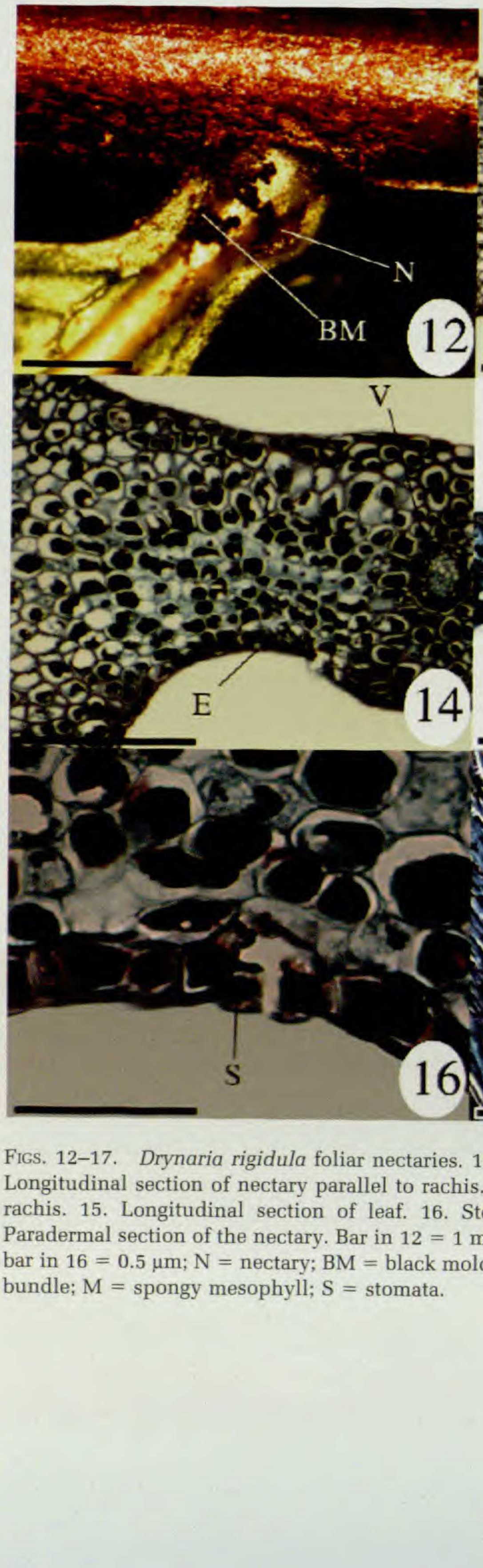
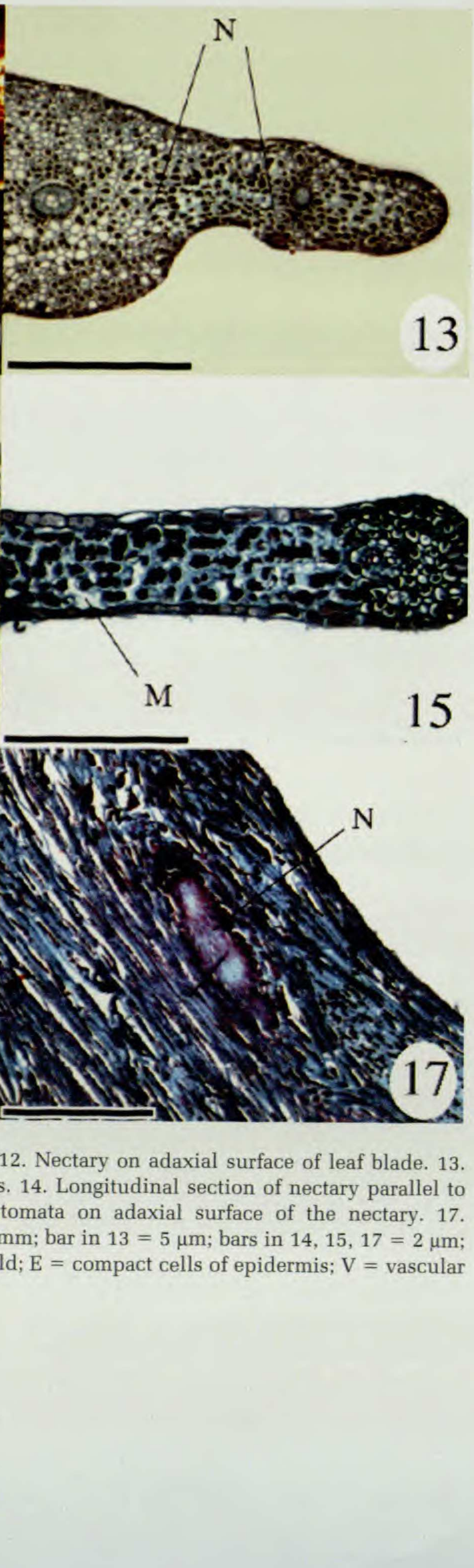
FIGS. 8–11. *Aglaomorpha coronans* foliar nectaries. 8. Longitudinal hand and section of nectary. 9. Longitudinal hand section of foliage leaf. 10. Longitudinal hand section of smaller nectary on leaf blade. 11. Longitudinal hand section of leaf. Bars in 8, 9, 11 = 2 μm; bar in 10 = 5 μm; N = nectary; I = intercellular spaces.

gland but its rim is formed by a secondary vein (Fig. 14). This vascular tissue consists of both xylem and phloem. Stomates occur on the abaxial surface of the nectary (Fig. 16). In paradermal section, the nectary is apparent from differences in the tissue staining (Fig. 17).

*Aglaomorpha acuminata*.—This species bears nectaries on specialized concave structures that are separate from the leaf blade as stand-alone structures. They are approximately 3 mm in diameter and occur at the base of each leaflet on the basiscopic side of the leaflet's junction with the rachis (Fig. 18). Less developed nectaries extend down the petiole even in the absence of leaflets. Clear liquid was observed on the abaxial surface of the nectaries (Fig. 18).

The anatomy of the nectary is complex in its composition and staining. Vertical sections show cellular zonation with a heavier staining glandular region surrounded by lighter staining non-glandular tissue (Fig. 19). Distinct from the leaf blade tissue (Fig. 20), the glandular cells are concentrated near the center of the protruding structure and non-glandular tissue makes up the







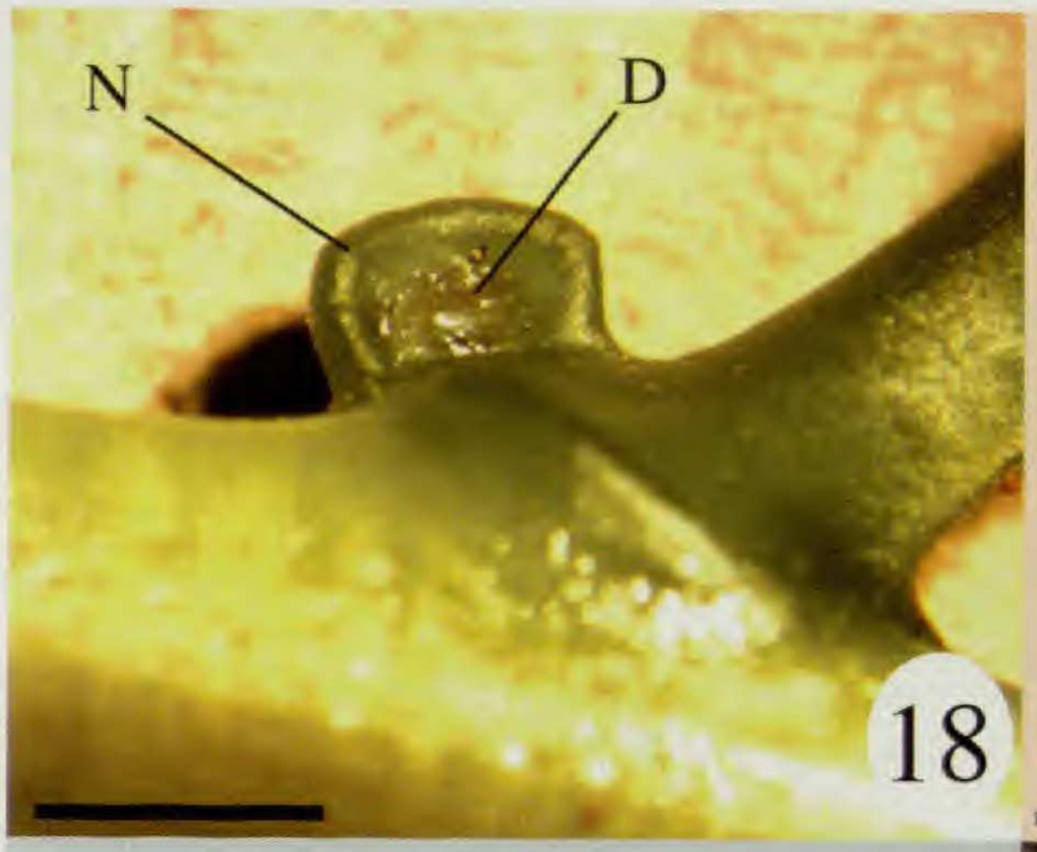


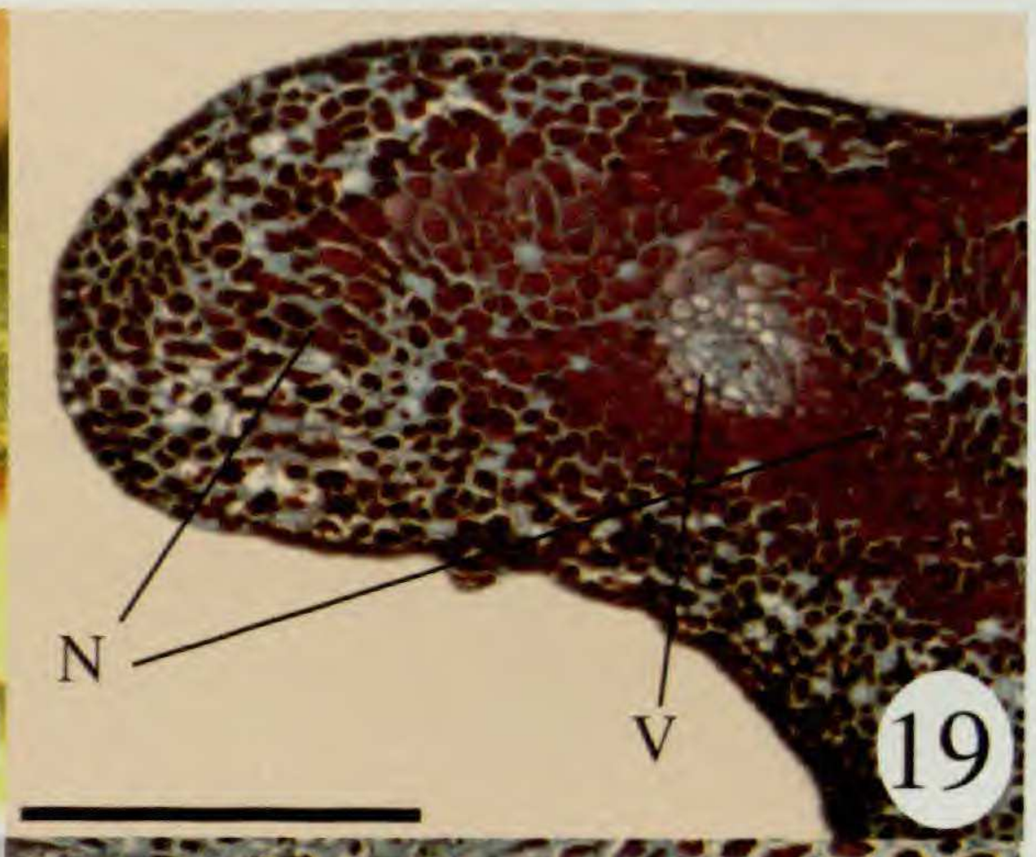


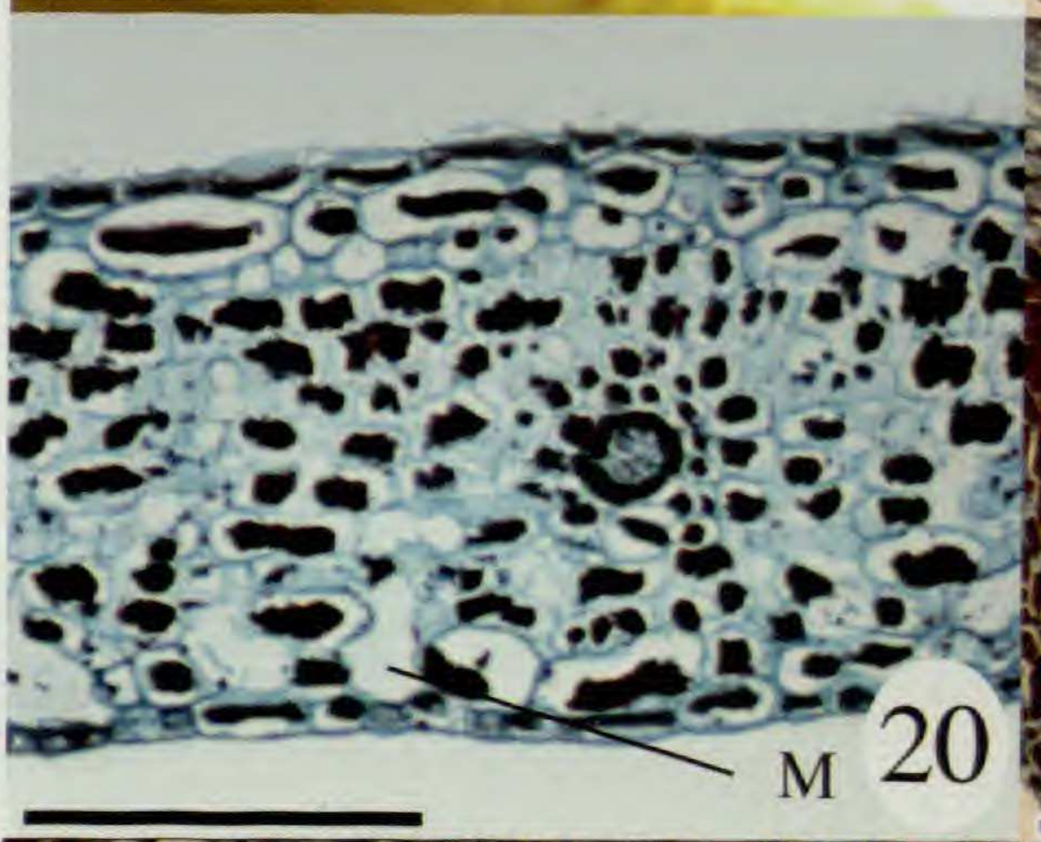


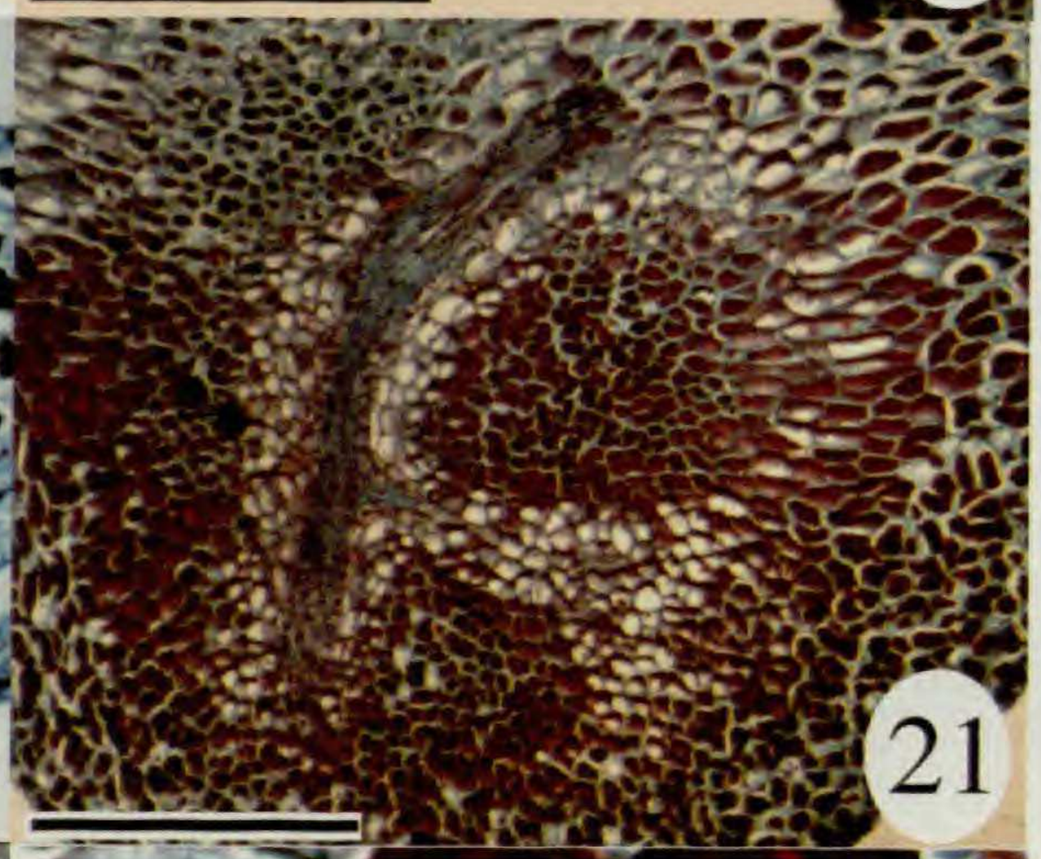


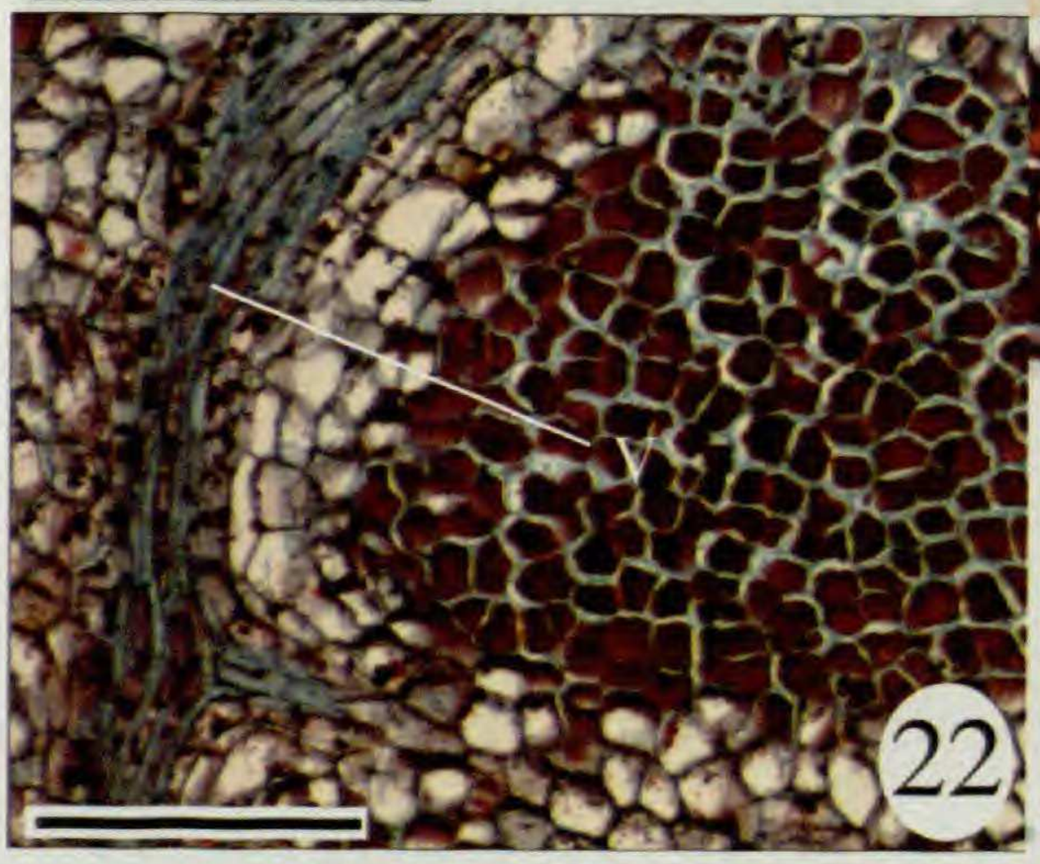

FIGS. 12–17. *Drynaria rigidula* foliar nectaries. 12. Nectary on adaxial surface of leaf blade. 13. Longitudinal section of nectary parallel to rachis. 14. Longitudinal section of nectary parallel to rachis. 15. Longitudinal section of leaf. 16. Stomata on adaxial surface of the nectary. 17. Paradermal section of the nectary. Bar in 12 = 1 mm; bar in 13 = 5 μm; bars in 14, 15, 17 = 2 μm; bar in 16 = 0.5 μm; N = nectary; BM = black mold; E = compact cells of epidermis; V = vascular bundle; M = spongy mesophyll; S = stomata.





FIGS. 18–23. *Aglaomorpha acuminata* foliar nectaries. 18. Nectary at the junction of the leaf blade to the rachis. 19. Longitudinal section of the gland perpendicular to the rachis. 20. Longitudinal section of the leaf. 21. Paradermal section of the nectary. 22. Paradermal section of the nectary. 23. Stomata and mold on the nectary. Bar in 18 = 3 mm; bars in 19, 21 = 5 μm; Bars in 20, 22 = 2 μm; Bar in 23 = 0.5 μm; D = droplet; N = nectary; V = vascular bundle; M = spongy mesophyll; S = stomata.

rim (Fig. 21). The leaf blade is composed of cells with green plastids and prominent intercellular spaces. Glandular region cells are approximately 0.18 μm smaller in diameter than those of standard leaf blade with non-green plastids. The tissue lacks prominent intercellular spaces. Vascular tissue branches within the nectary and is closely associated with the darkest staining tissue. In paradermal sections, the vein encircles the darker staining region and it is immediately surrounded by lighter staining cells (Figs. 21 and 22). Xylem and phloem are both present in the vascular bundle (Fig. 22). Stomates occur on the abaxial surface of the nectary (Fig. 23).

## Discussion

In most plants with nectaries, these structures are comprised of tissue that is small-celled, thin-walled and densely staining with reduced intercellular spaces compared to the surrounding tissue. These cells are often surrounded by sub-glandular tissue and by modified epidermal cells with a thick cuticle. The secretion of nectar may occur either through stomata on the epidermis of the nectariferous tissue or through epidermal cells or trichomes (Fahn, 1979; Elias, 1983).

Nectaries vary in their degree of vascularization according to taxa. These veins differ both in their proximity to the gland and in the composition of their tissue. Veins, when they occur, may consist of both xylem and phloem or only one of these. Often vascular tissue does not come into direct contact with the nectariferous tissue and ends in the subglandular cells. In the nectaries of other plants, vascular tissue may be entirely absent (Durkee, 1983; Elias, 1983). This specialization and variability in nectary vascularization, however, is often associated more with the size of the nectary than with its systematic specialization (Elias, 1983).

The nectaries of *Drynaria quercifolia*, *D. rigidula*, *Aglaomorpha acuminata* and *A. coronans* are anatomically similar in many features. They are vascularized glands composed of a region of densely staining cells that are smaller and more isodiametric than the surrounding non-glandular tissue. The nectariferous tissues have minute or absent intercellular spaces and vascular tissue is closely associated with the nectaries. This anatomical study is the first that has documented such a close association between nectaries and vascular tissue in ferns. All of the nectaries secrete nectar and have stomates in their abaxial epidermis.

Differences in the anatomy and distribution of the observed drynarioid nectaries are notable (Table 1). The nectaries occurring on *Drynaria quercifolia* and *A. coronans* are more similar to one another than to those of the other two species. *Drynaria quercifolia* and *A. coronans* nectaries occur as patches abutted by non-glandular leaf blade tissue and they are located mainly distal to the vein junction. Glands have also been observed basal to the veins (Zamora and Vargas, 1974; Chandra, 1980; Koptur *et al.*, 1982). In contrast, the glands of *D. rigidula* and *A. acuminata* are stand-alone structures separate from the leaf blade, occur consistently on and are restricted to the basiscopic side of the leaflet base. They continue down the petiole in absence of leaflets.

TABLE 1. Summary of results and nectary type classification.

| Species | Anatomy | Vascular tissue | Distribution |
|---|---|---|---|
| *Drynaria quercifolia* | Patch of densely staining cells | Abutting the nectary | Inconsistent. Mostly distal to the midvein-primary vein junction |
| *Aglaomorpha coronans* | Patch of cells | Abutting the nectary | Inconsistent. Mostly distal to the midvein-primary vein junction |
| *Drynaria rigidula* | Small concavity of densely staining cells | Forming the rim of the nectary | Restricted to the basiscopic side of the petiole |
| *Aglaomorpha acuminata* | Large spoon-like appendage of densely staining cells | Branching within the nectary | Restricted to the basiscopic side of the petiole |

Furthermore, the nectaries of *D. rigidula* are distinct in their reduction in size and *A. acuminata* nectaries are distinct in their large size (see scale bars in *Results* for size). The *A. acuminata* nectary is uniquely elaborate in comparison to any known fern nectary and is more similar to some angiosperm nectaries (Elias, 1983; Thadeo *et al.*, 2008, Zimmerman, 1932).

Despite similar pinnate leaf dissection and gland distribution, *D. rigidula* and *A. acuminata* occur on different branches of the cladogram (Fig. 24) (Janssen and Schneider, 2005). Therefore, these nectaries appear to be independently derived. Although *A. acuminata* nectaries are much more complex than those of the other drynarioid species in this study, further anatomical studies of other *Aglaomorpha* species will clarify the extent to which this complexity is shared within the genus.

Nectariferous patches, like those observed in *D. quercifolia* and *A. coronans*, are common throughout drynarioid ferns. The patches have also been observed in *A. heraclea*, *A. meyeniana*, *A. splendens* and *D. descensa* (Fig. 24) (Zamora and Vargas, 1974; pers. comm. Turner, 2006). *Drynaria rigidula* and *A. acuminata* are the only species, out of the four studied, with distributionally-restricted and stand-alone structures. Nectaries occur on various other species of ferns (Koptur, Smith and Baker, 1982), although relatively few anatomical studies of these glands have been conducted. Bracken (*Pteridium*) (Page, 1982; Power and Skog, 1987; Rumpf *et al.*, 1994) and *Cyathea* (pers. comm. White, 2007) are two examples of ferns with nectaries. The anatomy, ultrastructure and physiology of *Pteridium* nectaries have been described in detail. Similar investigations of the structure and function of drynarioid nectaries could be valuable.

*Pteridium* nectaries have been documented in great detail and are different from drynarioid nectaries in both distribution and anatomy. Bracken glands occur on the leaf axis (at the junctions of the stipe and midribs of the pinnae and also at the junctions of the midribs of the pinnae and the midribs of the pinnules). Drynarioid nectaries, in contrast, occur either on expanded leaf blades or on structures that remain on the petiole after foliar tissue has been reduced to form pinnate leaves. Anatomically, *Pteridium* nectaries differ from those of drynarioid ferns in that 1) vascular tissue does not form specialized

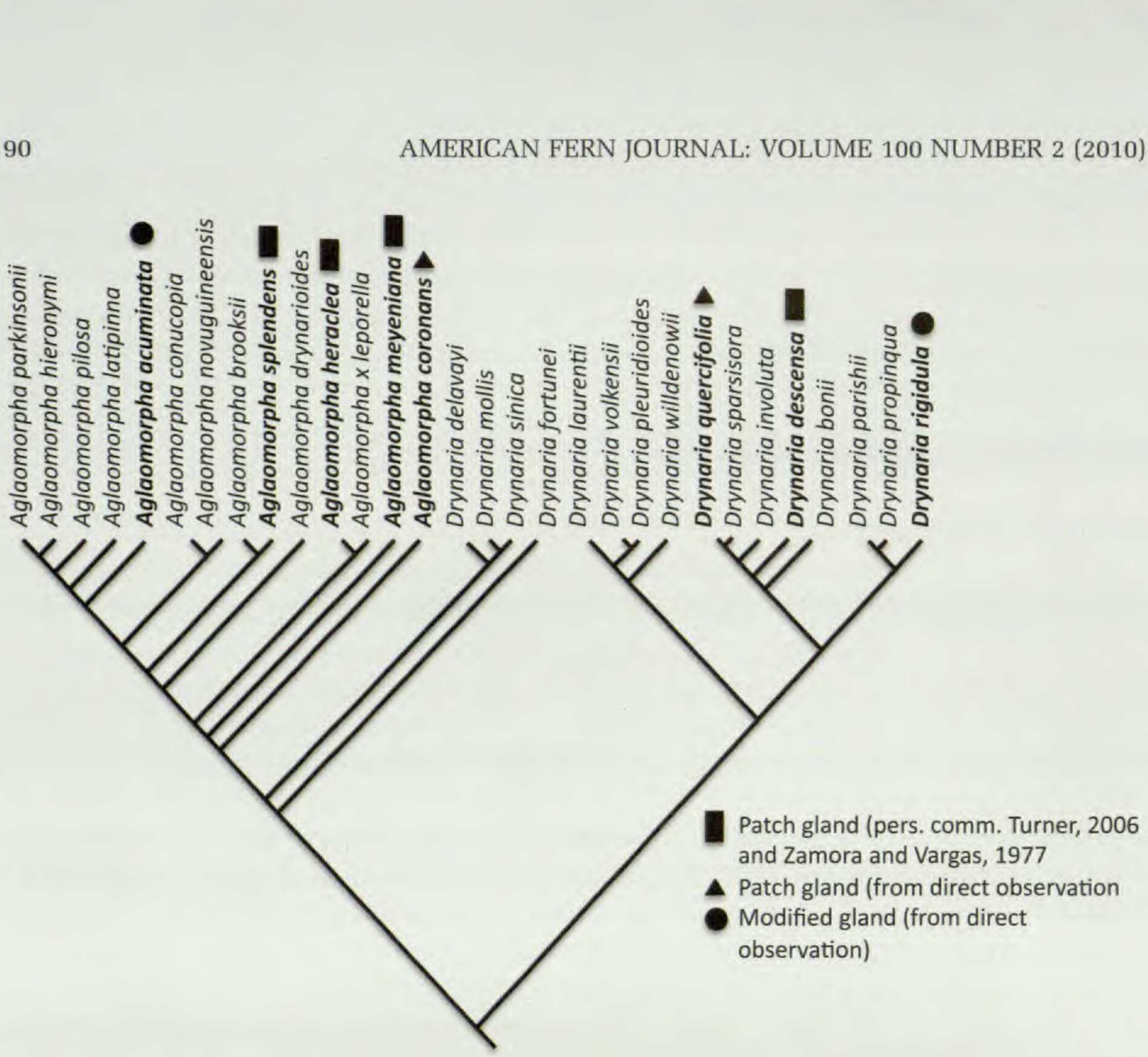



FIG. 24. Presence of nectaries on Janssen and Schneider's (2005) phylogenetic tree (used with permission).

branches abutting or extending into the nectary, 2) stomata are present in a greater abundance on the surface of the nectary, and 3) the nectariferous tissue has glandular and subglandular layers (Power and Skog, 1987; Rumpf *et al.*, 1994). Drynarioid glands are relatively simple in structure. Only in *A. acuminata* was zonation observed.

There are, however, some basic similarities between the nectaries of *Pteridium* and drynarioid ferns. Both nectaries are visible macroscopically and thus belong to the "structural" type as of extrafloral nectary (Zimmerman, 1932). They are both composed of tissue that is distinct from the surrounding parenchyma. As in the drynarioid ferns, the nectariferous cells of *Pteridium* are small, isodiametric, densely staining and associated with stomates (Power and Skog, 1987). Another similarity between the glands of the two groups is the decrease in secretory activity as the gland ages and matures (Power and Skog, 1987; Rumpf *et al.*, 1994). Although this study did not examine the anatomy of nectaries at different ages, active nectaries were absent on older portions of fronds.

## CONCLUSIONS

Detailed anatomical data help clarify phylogenetic analyses (Elias, 1983; Stuessy and Crisci, 1984), and this purpose is one possible application for the

anatomical differences and similarities of drynarioid fern nectaries. The most recent study of the two genera combines morphological and molecular data to conclude that *Drynaria* is paraphyletic and *Aglaomorpha* is monophyletic (Fig. 1) (Janssen and Schneider, 2005). However, the morphological data set *alone* contradicts the molecular evidence and the study does not reject the null hypothesis of a monophyletic *Drynaria*. Adding an anatomical analysis of drynarioid nectaries throughout the genera may further clarify the phylogeny of *Drynaria*.

Although the nectaries of only four drynarioid species were examined, the data contribute significantly to the anatomical knowledge of these glands. The presence of vascularized nectaries composed of cells lacking prominent intracellular space was observed. The glands are distinct from the surrounding tissue and the similarity in anatomy and distribution of the nectaries of *D. rigidula* and *A. acuminata* may be independently derived. Contrary to the only previous anatomical description, drynarioid fern nectaries are not composed of columnar cells and although they are vascularized, they are not associated with a central vascular plexus, as reported (Nayar, 1961). The *Aglaomorpha acuminata* nectary is unique among known ferns in its anatomical complexity. Future studies should consider surveying other taxa, such as *Pleopeltis*, and implementing different staining techniques.

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